Survival rates of Malayan rats

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INFORMATION CONCERNING the expectation of life of wild animals, whether from birth or from any point before or after they become adult, is notoriously difficult to obtain. Human life tables, such as those computed by Pearl (1930), are based on the great mass of precise statistical data made available by census returns, but only very occasionally is it possible to obtain comparable information about a wild animal species.

Examples of work based on such data are summarised by Deevey (1947), and include observations on wild sheep based on skulls left by wolves, on birds ringed as nestlings and on fish and barnacles. Usually, however, far less information is available. The records of ages reached by animals in captivity, summarised by Flower (1931), probably represent only the probable maximum age attained by the species under artificial and sheltered conditions, and have not much relevance to the survival rates of wild animals.

Another approach to the problem is through the data obtained from the recapture of marked animals, data which are often exceedingly difficult to interpret. One of the most comprehensive works based on this method is that provided by Leslie *et al* (1953) who, having developed an equation in general terms, substituted values from marking experiments to obtain parameters representing the life of a wild population. The method, as presented, does not seem to apply to the data presented here, which are derived from continuous trapping by a moving line of traps, and, owing to this, and to what Bodenheimer (1938, p. 30) has called "the mathematicophobia of most biologists", an analysis by this method has not been attempted.

Material and Method. During the last six years, information about the life history of Malayan rats has been accumulated from three sources: (*a*) the examination of large routine collections made primarily for parasite surveys, (*b*) mark and recapture experiments, and (*c*) the keeping of animals in captivity. The areas from which collections were made and in which marking experiments have been performed, details of the techniques used, and notes on the species have been given by Audy and Harrison (1953), and by Harrison (1955). A popular account of the marking technique was given by Harrison (1951b). Mark-recapture experiments have been carried out in six areas which are designated in the text by their laboratory names of: "Forest", an area in primary and secondary forest; "Pylon", "House", and "Stream", areas of grassland and scrub near forest edge; and "Taylor Road" and "Spooner Road", suburban areas of garden and scrub. These areas and those in which routine collections were made are all within a radius of about twenty-five kilometres of Kuala Lumpur.

In the present paper this information is treated as follows. Data from marked rats of known ages and from captive animals is assembled to give estimates of weights at various ages. These are applied to the records of trapped rats to obtain an estimate of the age distribution and hence the survival rate. Data from mark-recapture experiments are studied directly to produce an estimate of survival rates. These survival rates are compared with one another and correlated with the reproduction rates of the same animals estimated by Harrison (1955).

The animals considered here are of the following species and forms:—

Chiropodomys gliroides (Blyth), Pencil-tailed Tree-mouse.

Rattus rattus diardii (Jentink), Malaysian House-rat.

R.r. argentiventer (Robinson & Kloss), Ricefield Rat.

R.r. jalorensis (Bonhote), Malaysian Wood-rat.

R.r. jarak (Bonhote), Jarak Island Rat.

R. exulans (Peale), Little Burmese Rat.

R. mülleri (Jentink), Müller's Giant-rat.

R. bowersi (Anderson), Bower's Giant-rat.

R. whiteheadi (Thomas), Lesser Spiny-rat.

R. rajah (Thomas), Rajah Spiny-rat, comprising two forms R.r. surifer (Miller) and R.r. pellax (Miller) which may or may not be distinct.

R. canus (Miller), Grey Tree-rat.

R. sabanus (Thomas), Long-tailed Giant-rat.

Climate and growth. The climate of central Malaya is remarkably constant, compared with other parts of the world. Fig. 1 shows a temperature humidity diagram
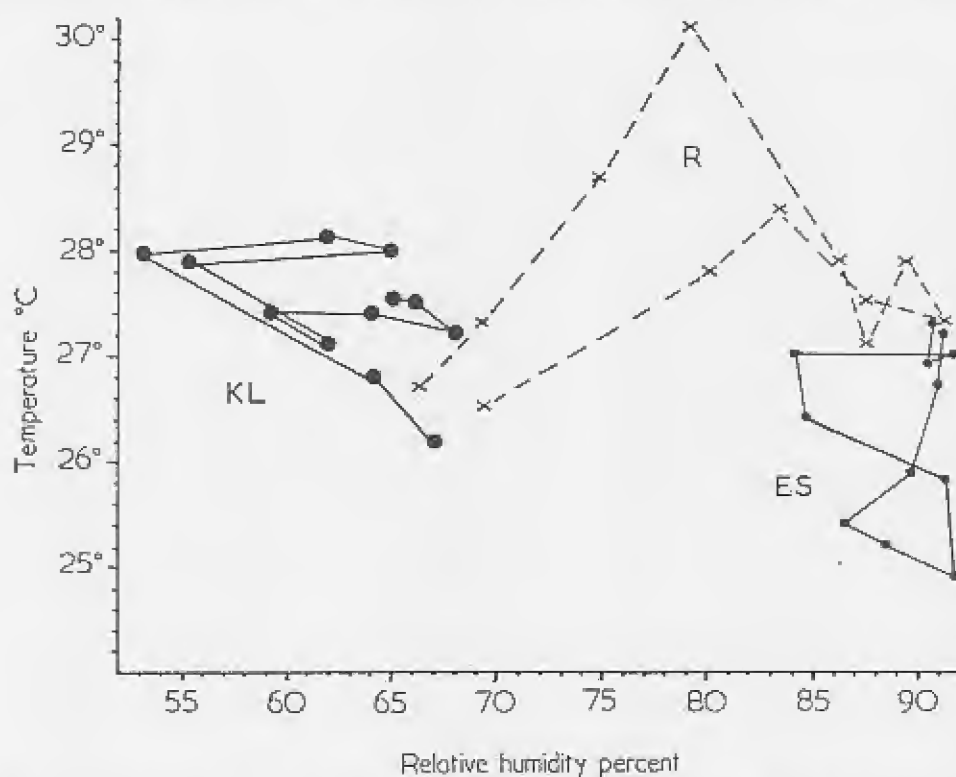

Fig. 1. Temperature—humidity diagrams. Mean temperatures and relative humidities plotted month by month for Kuala Lumpur Aerodrome (KL) 1951; Espiritu Santo (ES) 1933–4, in forest; and Rangoon Docks (R) 1938. Temperatures are means of daily maxima and minima, humidities means of daily readings in early afternoon. The pronounced difference between Kuala Lumpur and Espiritu Santo reflects the difference between cleared land and forest.

(hythergraph) of Kuala Lumpur Aerodrome for 1951 compared with one for Hog Harbour, Espiritu Santo (in the New Hebrides), for 1933–4 as given by Baker and Harrisson (1936). The latter is regarded as a classical example of a uniform tropical climate, and it will be seen that the Kuala Lumpur diagram is of similar range, although of different absolute value. The humidity at Espiritu Santo, however, was measured in forest while that at Kuala Lumpur was measured in a Stephenson's screen over grass. For comparison the diagram for Rangoon, Burma, with a typically monsoon climate, is also included in the figure.

It is sometimes rashly assumed that breeding of animals will bear no relation to season in such uniform climates. Breeding seasons have however been demonstrated in the New Hebrides (Baker 1947), and are known for Bornean and Malayan birds (Gibson-Hill 1952), while unpublished data suggest that Malayan bats exhibit some such season as those described from the New Hebrides by Baker and Baker (1936) and Baker and Bird (1936). It has also been shown that male rats undergo an annual cycle of sexual activity, although this does not appear to be sufficient to affect the pregnancy rates of the females (Harrison 1955). Nevertheless in rats there appears to be no breeding season, although breeding activity may show fluctuations related to rainfall (Harrison 1952). In climates where there is a breeding season there will be of course be an annual change in the age distribution of the population, and this will be reflected as an annual change in the weight distribution. Furthermore there may be annual variation in the weights of adults, as was noted with shrews in England by Middleton (1931) (although such a change was not found in rabbits by Brambell, 1944). In Malaya, however, with its uniform climate and continuous breeding throughout the year, there appears to be no seasonal variation in growth rates, or in the age distribution of the population, and in the absence of any violent fluctuations of population brought on by epizootics, or clearing of forest, it appears legitimate to consider populations of Malayan rats as stable ones, having a constant age structure, and composed of animals having similar growth rates. It is therefore possible to relate size to age in a way not possible in a more markedly seasonal climate.

Age and weight. The history of the growth of a rat appears to be that it grows fairly continuously and evenly, up to a certain size, and then, for the rest of its life, fluctuates about that size. Such a history is a commonplace for a rat in captivity, as, for example the *R.r. diardii* shown in fig. 2. A similar curve for the Indian Mole Rat (*Bandicota bengalensis*) was published by Harrison and Woodville (1950).

No marked wild rat has yet been trapped sufficiently frequently in the early part of its life to produce a wholly comparable growth curve, but the results which have been produced indicate a similar trend. It was not found possible to make regular measurements of sample lengths, and the measurement has been confined to weight, a dimension unsatisfactory in that it is easily affected by hunger and pregnancy, but one easy to measure with fair accuracy. To encourage uniformity the weight was always taken on the morning after the rat was trapped, before any food was offered, although water was given.

Examples of the observed growth of *Rattus rattus jalorensis* are shown in fig. 3. For only two rats was the rat marked at birth and subsequently recovered, one at 40 days old, the other at ten months and on a number of following occasions. These two however provide a framework to which the recorded growths of other rats can be fitted, as are the five shown in fig. 3. Many more can be fitted, but this figure is limited to
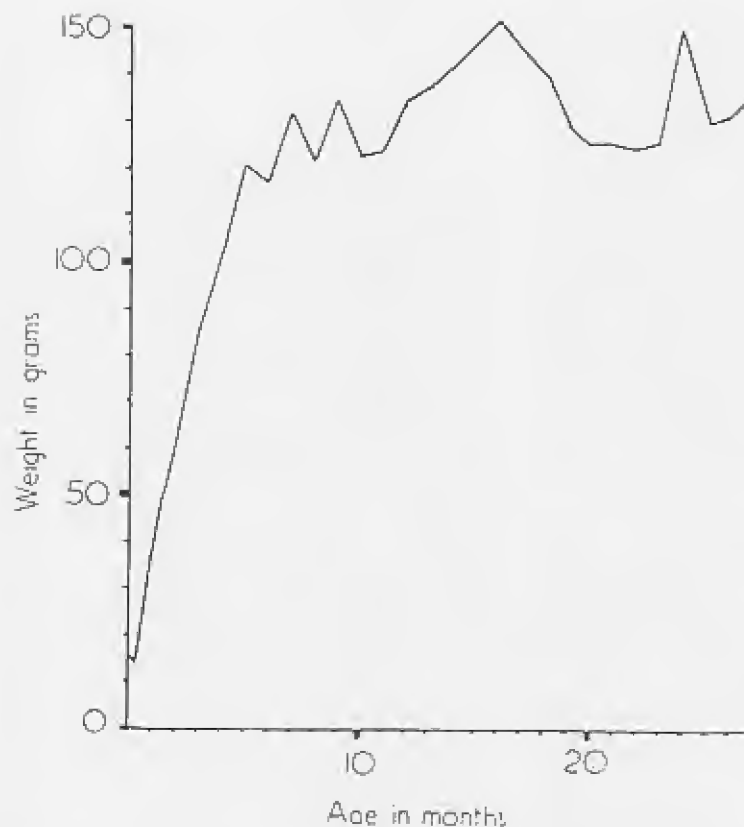
Fig. 2. Growth of captive *R.r. diardii.* Record of weight, month by month, of a captive specimen
of the Malaysian House Rat. This species is chosen because it appears to adapt itself
well to captivity.

seven rats only to avoid confusion. By fitting together results in this way it is possible
to produce an "average" curve of weight and age for the species. From this curve it is
possible to read off an approximate median weight for any age and also an approximate
median age for any weight.[1] The latter, however, will be liable to large errors in the
higher weight groups where the curve flattens. Such curves have been constructed for
the species shown in table 1, being based in each case on weighings of marked rats
which have been followed through for a considerable part of the early part of their lives.
Only with *R.r. jalorensis,* however, has the marking at birth and subsequently recovery
of the grown rat been successfully accomplished. The growth for the first two months
of lives of other species is derived from caged animals.

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[1]. The age-weight estimate is, strictly, a point on the median curve of a set of curves, and does
not necessarily represent either the median weight at a given age, or a median age at a given weight.
Were the relation of weight to age linear, and were the distribution of rats uniform by age, then the
age-weight estimate would represent both of these values. With the somewhat approximate methods
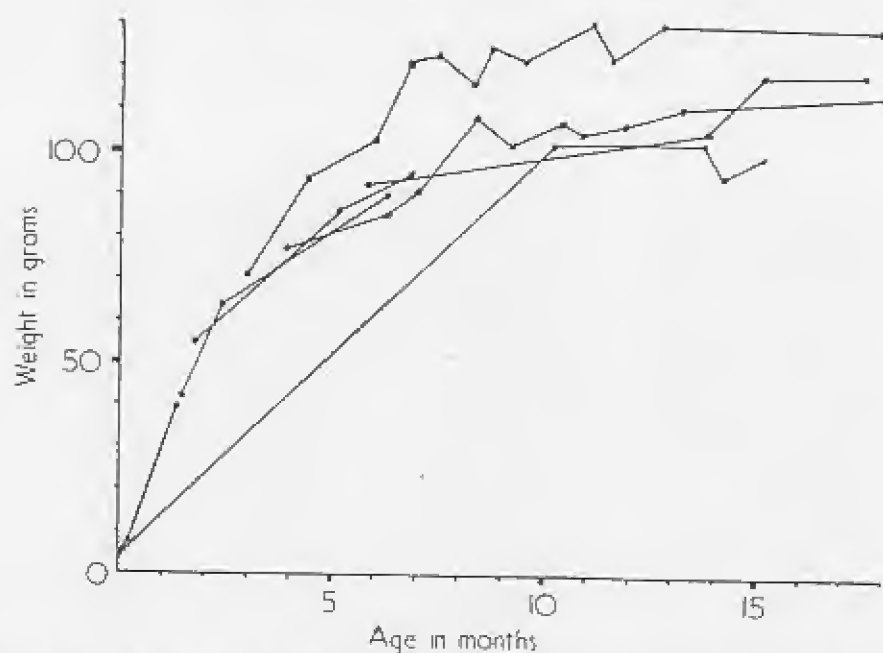used, no great error is introduced by assuming this to be so.

Fig. 3. Growth of wild *R.r. jalorensis*. Records of the weights at successive captures of seven marked specimens of the Malaysian Wood Rat from Spooner Road experimental area. Only two of them were marked as nestlings, the remainder are entered at appropriate points.

TABLE 1

AGE AND WEIGHT

Median weights of wild marked rats, month by month.

Age Months		R.r. jalorensis	R.r. argentiventer	R. exulans	R. mülleri	R. whiteheadi	R. rajah
1	..	30g.	25g.	13g.	45g.	20g.	30g.
2	..	55	50	25	110	35	50
3	..	75	70	33	180	42	70
4	..	85	85	37	220	47	85
5	..	90	95	39	240	51	100
6	..	95	105	41	250	53	110
7	..	—	115	—	260	55	120
8	..	—	122	—	270	—	130
9	..	—	—	—	290	—	140
10	..	—	—	—	300	—	147
11	..	—	—	—	310	—	155
12	..	—	—	—	320	—	160

Such curves cannot be regarded as highly accurate estimates of the median, and so it is probably sufficient if the weights are recorded, for convenience in subsequent use, to the nearest apropriate weight-group.

For other rats less complete data are available, and the estimates of median weight, for what they are worth, are set out in table 2. For all but the *R.r. jalorensis* from oil palms, these figures are derived from the growth of rats in captivity supplemented by information from marked rats in the case of *R. sabanus*. The oil-palm rats form a population with peculiarities of its own, as pointed out in a former paper (Harrison, 1951). One of these peculiarities is that the maximum weight attained is consistently lower, being some 85 per cent to 90 per cent of that attained by the same species from forest and wasteland. It has not been possible to mark rats from this locality, and the weights given in the table are derived by assuming that all weights are 85 per cent to 90 per cent of those for corresponding ages of other specimens.

TABLE 2

AGE AND WEIGHT

Median weights of rats in captivity month by month. *R.r. jalorensis* from oil palm estimated from Table 1.

Age Months		Chiropodomys gliroides	R.r. diardii	R.r. jalorensis (oil palm)	R. bowersi	R. sabanus	R. canus
1	..	3g.	35g.	25g.	60g.	50g.	40g.
2	..	6	60	50	150	120	70
3	..	8·5	85	65	250	180	90
4	..	11	100	75	270	200	110
5	..	12·5	115	80	290	220	130
6	..	13·5	120	85	310	235	140
7	..	14·5	—	—	330	250	140
8	..	—	—	—	340	265	145
9	..	—	—	—	350	275	150
10	..	—	—	—	—	285	155
11	..	—	—	—	—	295	160
12	..	—	—	—	—	300	165

Estimation of age-distribution from weight distribution. In the routine collections of animals made up to the end of 1952, care was taken to ensure that as far as possible, rats were trapped indiscriminately, and there is little evidence that, in the circumstances, there is any particular bias towards young or old rats, or males or females. Such evidence of bias as can be discovered is discussed by Harrison (1955), and chiefly involves the escape of young specimens through the mesh of the traps.

If these collections are taken as a fair sample of the population, then it is possible to apply the median weights at different ages, from tables 1 and 2, to the observed weights, and obtain an estimate of the age distribution of the population. The simplest and most familiar way to demonstrate the age distribution is to construct a life table. The construction of a life table is explained in most works dealing with the statistics of human populations, such as Pearl (1930) and Bradford Hill (1950). In principle it follows the life of a group of individuals all of the same age, and shows the number that will be alive at ages 1, 2, 3, 4, etc. It is constructed by taking the actual number of

individuals in the population as being the number in the group which start at age 0, and then showing successively the number which have survived to age, 1. 2, 3, 4, etc., the number surviving to age 4, for example, being the number in the population of ages 4 or more.

This has been done graphically in figures 4, 5, and 6, where each entry is shown as a point on a diagram with ages in months reading horizontally, and actual numbers shown vertically on a logarithmic scale. A logarithmic scale is chosen so that the same gradient indicates the same death rate at different points of the curve and the steeper the gradient the higher the death rate. It is remarkable that the series of points lie very close to straight lines, indicating that the death rate is constant over the range of ages considered. Straight lines, fitted by eye, have been drawn in.

Fig. 4 shows the lines for the five species of forest rat, *R. sabanus*, *R. rajah*, *R. mülleri*, *R. canus*, and *R. bowersi*. The last two species, indicated by broken lines on the diagram, are represented by only small numbers and are plotted on a scale equivalent to one tenth of that shown (i.e. 1,000 on the scale represents 100 rats). All specimens of both forms of *R. rajah* are consolidated because of the large number of younger specimens which can only doubtfully be allotted to either *surifer* or *pellax*.
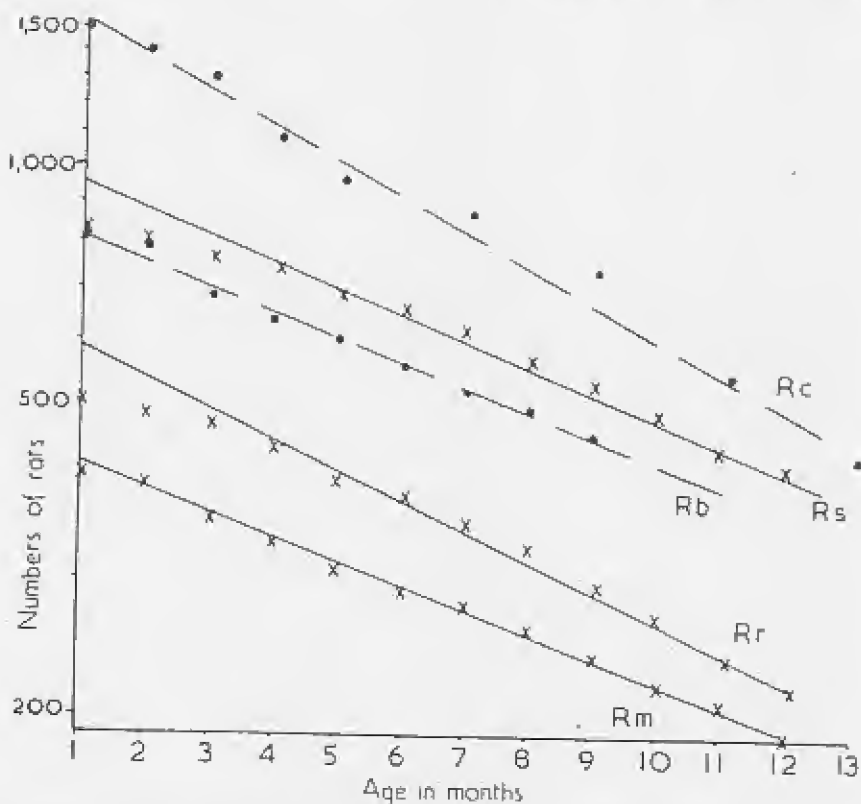

Fig. 4. Survival from the weight distribution, forest species. Total numbers of rats (logarithmic scale) examined during 1948–52, of weight greater than that corresponding to the age shown on the horizontal scale. Continuous lines (x, x.), numbers as scale:—Rs, *R. sabanus*; Rr, *R. rajah*; Rm, *R. mülleri*. Broken line (dots), numbers one tenth of scale:— Rc, *R. canus*; Rb, *R. bowersi*.

Fig. 5 shows the subspecies of *R. rattus*: *R.r. argentiventer*, *R.r. jarak*, *R.r. jalorensis*, and *R.r. diardii*. *R.r. jalorensis* is divided into the two populations from oil palms and from "Forest" (i.e. other localities, mostly secondary forest and scrub). It will be seen that the oil-palm rats exhibit a decidedly lower death rate. The *R.r. diardii*, all from Kuala Lumpur town, are divided into the two sexes, since the species is the only one which exhibits any difference in the rate between sexes. It will be seen that the males exhibit a decidedly higher death rate than the females, a conclusion which was reached, on other grounds, in an earlier paper (Harrison 1951a). The *R.r. jarak* were collected on two visits (January 1950 and 1953) to Jarak Island in the Straits of Malacca. This rat appears to be a feral form of *R.r. diardii* but slightly smaller, midway in size between *diardii* and *jalorensis* (Audy *et al.* 1950). The weights at different ages used were the means of those for *diardii* and *jalorensis*.

Fig. 6 shows the remaining three small rats, *Chiropodomys gliroides* from forest, *R. exulans* mostly from grassland and the forest clearings of the aborigines, and *R. whiteheadi* mostly from forest.
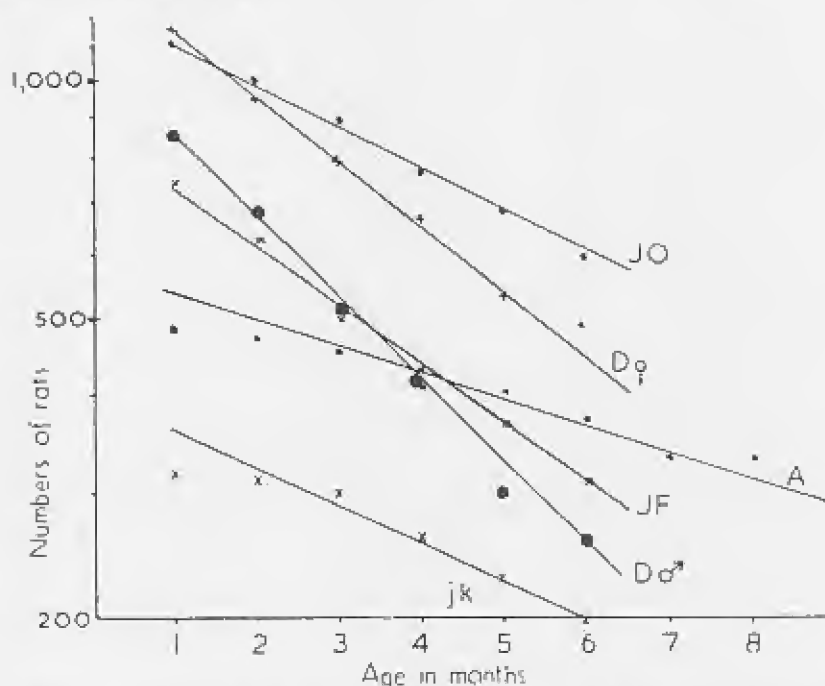

Fig. 5. Weight distribution, forms of *Rattus rattus*. As figure 7, numbers (log. scale) of over the age shown. JO (dots), *R.r. jalorensis* from oil palm; JF (x), *R.r. jalorensis* from forest and scrub; D ♀ (x) *R.r. diardii* females, D ♂ (large dots) males; A (dots), *R.r. argentiventer*; jk (x) *R.r. jarak* from Jarak Island, sample collected on two occasions January 1950 and January 1953.

If the death rates of these rats are really constant over the whole range, that is to say if the points really lie on straight lines, then for each rat we can determine a death rate, or, more conveniently a survival rate (since *survival rate* = 1 *minus death rate*) from the slope of the line. If N is the total sample, and if s is the constant survival rate per month, then starting at zero, Ns is the number one month old and over, Ns^2 the

number two months old and over, Ns^3 the number three months old and over, and so on. Since numbers are plotted on a logarithmic scale, they will lie on a straight line the slope of which will give the value of s the survival rate. In table 3 these survival rates are summarized, and expressed also in the alternative form of "mean length of life"[1], read directly from the diagram as the time by which any population N sinks to N/e.

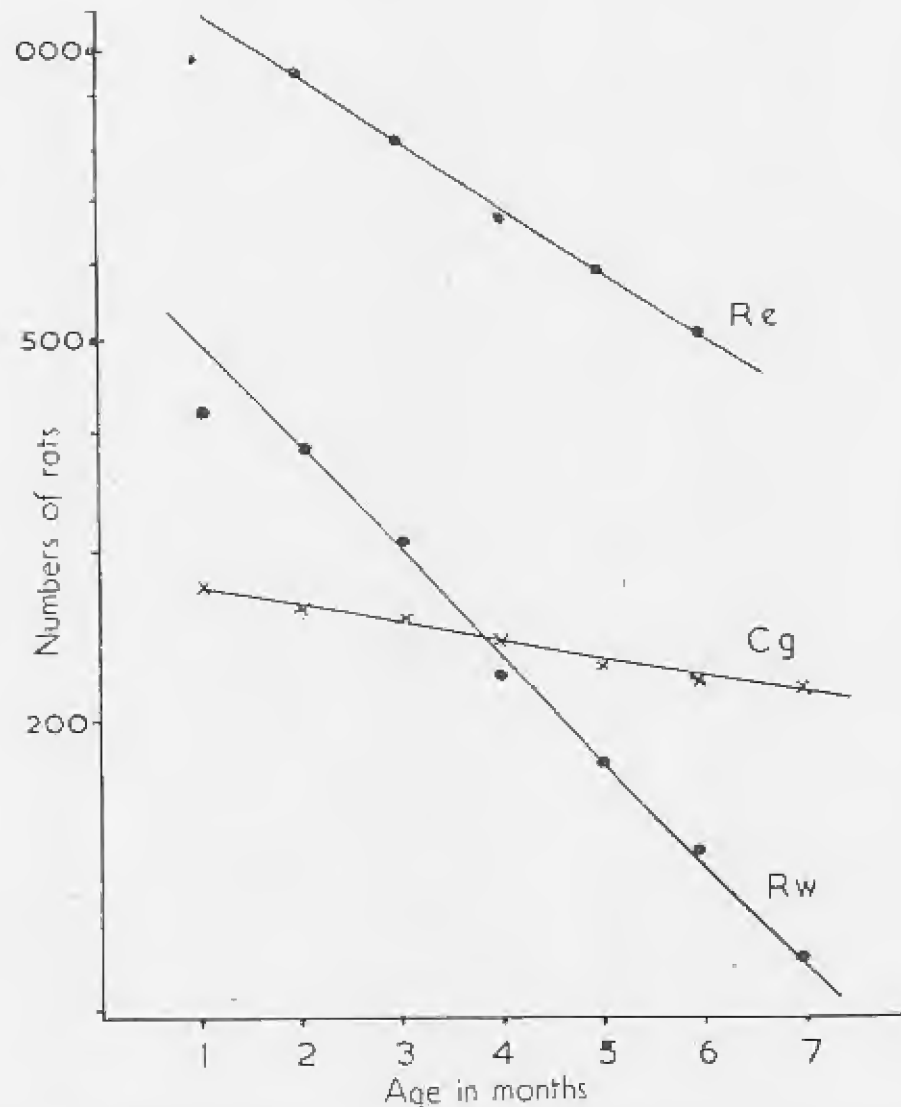Fig. 6. Weight distribution, other species. As figs. 7 and 8. Re (dots), *R. exulans*; Cg (x), *Chiropodomys gliroides*; Rw (dots), *R. whiteheadi*, largely from forest but also from scrub.

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1. Mean length of life $= 1/\log s$, since if the survival rate is constant the aggregate number of months lived by N rats will be $\int Ns^t dt$. The number alive at the mean length of life will be N/e.

TABLE 3

SURVIVAL ESTIMATE FROM WEIGHTS

Survival, as mean length of life and as a rate per month, calculated by applying the estimates of weights at ages to the records of the weights of all rats collected from 1949 to 1952 as in figures 4–6.

Species				Number	Mean length of life in months	Survival rate per month
Chiropodomys gliroides	..		..	272	23·8	0·96
R.r. diardii ♂ ♂	..	..	..	851	4·4	0·80
♀ ♀	..	..	..	1149	5·2	0·83
R.r. jalorensis						
Forest	..	..	..	..	739	6·0	0·85
Oil Palm	..	..	..	1111	8·3	0·89
R.r. argentiventer	..	..	..	480	13·1	0·93
R.r. jarak	..	..	..	..	298	9·0	0·90
R. exulans	..	..	..	977	6·3	0·85
R. mülleri	..	..	..	409	14·0	0·93
R. bowersi	..	..	..	82	14·0	0·93
R. whiteheadi	..	..	..	421	4·0	0·78
R. rajah	..	..	..	..	501	11·4	0·92
R. sabanus	..	..	..	832	13·2	0·93
R. canus	..	..	..	..	151	9·7	0·90

In making the estimates it would clearly not be correct to say that all rats of, say, more than a particular weight were of more than the corresponding age; there are clearly a number of rats (X) of greater age but of less weight, and another group (Y) of less age but greater weights. Since, however, the estimate is of median weight and median age, then X and Y represent approximately equal numbers of rats, and it is therefore approximately true to say, that the *number* of rats of more than a certain age is equal to the *number* of rats of more than the corresponding weight. This would only be strictly true if the age distribution were uniform, and the age-weight relationship linear. Since the number of rats decreases with age, then Y tends to be greater than X, and since the weight does not increase uniformly with age, X tends to be greater than Y. Although the errors act in opposite directions they are not constant, and the net effect will be to over-estimate the numbers in the higher age groups.

Very young rats are either not trapped or can escape from the mesh of the traps used, so that the figures for the first few months of life will also be underestimated.

The most serious source of error, however, is likely to be the faulty estimate of the median weight at a given age. These are likely to be underestimated, and the survival rate overestimated, from the very nature of the information on which they are based. Weights derived from the trapping of marked rats will be unduly influenced by rats trapped frequently, and such rats are known to lose weight in the traps. Weights derived from rats kept in captivity are likely to be too low if the rat does not respond well to captivity. An observation of this sort is made by Leslie *et al* (1952) who say "Evidently age for age the adult wild rat may achieve a much higher level of weight than that observed in the laboratory".

Survival of young marked rats. Although the age-weight estimate does not give an accurate estimate of the actual age of the older rats, it does give a reasonable one for the younger rats, which are growing quickly. It may, therefore, be used to estimate the age of marked rats when these have been marked early in life, but is of no value for estimating the age of grown rats, marked later in life.

Tables 4 and 5 show the results of marking 189 *R.r. jalorensis* and 134 *R. exulans* of various sizes from three areas (Pylon, Stream and Spooner Road). Not all rats marked are considered, but the groups were made comparable by selecting all the younger (lighter) rats, and for each young rat so selected including the data of the next older rat to be marked of weight over 85g for *R.r. jalorensis* (10 very young rats not so balanced), and of weight over 33g for *R. exulans*. The tables show, for each weight group, the number of rats marked, and, month by month, the numbers subsequently recovered for the next four months. The number recovered is shown, not as the number actually recovered during the month, but as the number "known to have survived" i.e. the number recovered during the month or subsequently. Thus of the 35 *R.r. jalorensis* marked at a weight of between 30 and 54g (corresponding to an age of between 1 and 2 months) 21 were recovered either during the month following markings, or subsequently, and are shown as known to have survived to age 2 months. Of these 17 were recovered during the month next but one, or subsequently, and are shown as known to have survived to age 3 months. The survival rate from age 2 months to age 3 months is therefore 17/21 of these rats, and 2/3 of the rats marked a weight group smaller, an average rate of 19/24.

<p style="text-align:center">TABLE 4</p>

<p style="text-align:center">AGE AND SURVIVAL RATE</p>

Numbers of *R.r. jalorensis* known to have survived up to 4 months after marking at an age estimated from the weight.

Marked at:

Age (months)		Weight group	Number marked	Number known to have survived to ages from 1 to 7 months						
				1	2	3	4	5	6	7
0	.. under	30g.	10	4	3	2	2	—	—	—
1	..	30–	35	—	21	17	13	11	—	—
2	..	55–	35	—	—	22	19	18	14	—
3	..	75–	19	—	—	—	14	11	11	9
4+	..	85 and over	90	—	—	—	—	60	42	35

<p style="text-align:center">TABLE 5</p>

<p style="text-align:center">AGE AND SURVIVAL RATE</p>

<p style="text-align:center">Records for R. exulans as at Table 4</p>

Marked at:

Age (months)		Weight group	Number marked	Number known to have survived to ages from 1 to 7 months						
				1	2	3	4	5	6	7
1	..	13–	26	—	17	10	8	5	—	—
2	..	25–	39	—	—	30	25	17	12	—
3	..	33–	25	—	—	—	13	9	6	4
4+	..	37 and over	44	—	—	—	—	23	17	12

In table 6 the consolidated survival figures, month by month, are compared with the figures "expected" if the survival rate were constant, whatever the age, and equal to the average, i.e. 207/257 for *R.r. jalorensis* 125/127 for *R. exulans*. Clearly the observed and expected numbers of survivors agree very closely, and a chi-squared test gives probabilities of about 50 per cent and 40 per cent respectively that the differences found are due to chance. There is, therefore, no detectable difference between the survival rate of young and of older specimens of these species.

TABLE 6

AGE AND SURVIVAL

Chi-squared test applied to the known numbers of survivors at each month, from the figures of tables 4 and 5.

Age	Number present	*R.r. jalorensis* Survivors obs.	exp.	Chi-squared	No. present	*R. exulans* Survivors obs.	exp.	Chi-squared
1–2	4	3	3.2	—	—	—	—	—
2–3	24	19	19.4	0.002	17	10	12.1	1.3
3–4	41	34	33.1	0.1	40	33	28.6	2.4
4–5	46	40	37.1	1.2	46	31	32.9	0.4
5–6	89	67	71.7	1.5	49	35	35.0	0.0
Over 6	53	44	42.7	0.3	23	16	16.4	0.3
Total	257	207		3.1	175	125		4.1
				P = 0.5				P = 0.4

Unfortunately there are insufficient data for young specimens of other species of rat to produce comparable figures, but such figures as are available do not suggest any differences of survival rates.

It seems legitimate to suggest, therefore, that the survival rate of rats big enough to be trapped is not affected by age, and that data for all rats of the one species (in the same conditions) may be consolidated.

Estimation of Survival Rate of marked rats. If the survival rate is, in fact, not influenced by age over the range considered, then the mean survival rate of the marked rats may be estimated easily and quickly, by plotting the numbers recovered after periods of 0, 1, 2, 3, etc. months on a logarithmic scale of numbers. These points should then lie on a straight line, the slope of which will give an estimate of the mean survival rate, in the same way as did the lines derived from the age weight relationship.

Consider a population of N marked rats, and let the chance of recovery of a marked rat at all (any number of times) be p; then the total number of rats recovered after marking will be Np.[1] That is Np will be the number recovered during the first month or subsequently. If the survival rate is s per month, then the number of marked rats in existence at the beginning of the second month will be Ns and therefore the

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[1]. It is assumed here that p is constant since it depends on the trapping rate, which is constant, and the presence of the rat in the area, the chances of which, if the survival rate is the same for all ages, is also constant. The possibility that it may be affected by the reaction of the rat to trapping is discussed below, "Possible errors, 5".

number of marked rats recovered during the second month or subsequently will be Nsp. For the third month, the number at the beginning will be Ns^2 and the number recovered Ns^2p. The number of rats marked, and the numbers recovered during or after the first month, the second month, the third month, and so on will therefore form a series: N, Np, Nps, Nps^2, Nps^3, Nps^4 . . . From the second term onwards this series diminishes by a uniform proportion, s, and by plotting these points on a logarithmic scale of numbers s can be estimated. The first term N, the number marked, does not fit the series, (unless p happens by chance to be equal to s) and is not considered in fitting the regression lines.

Figures 7, 8, and 9 show all the available information plotted. The scale of numbers is logarithmic, and the scale of months is linear. The point opposite zero months is the number marked (N), that opposite month one is the total number recovered (during the first month and onwards, Np), that opposite month two is the total number recovered from the second month onward. (Nps), and so on. It will be seen that with the exceptions of $R.r.$ *argentiventer* and $R.$ *sabanus*, the number marked (N) does, in fact, lie close to the regression line drawn through the other points. The two exceptions presumably have an unusually low value of P.
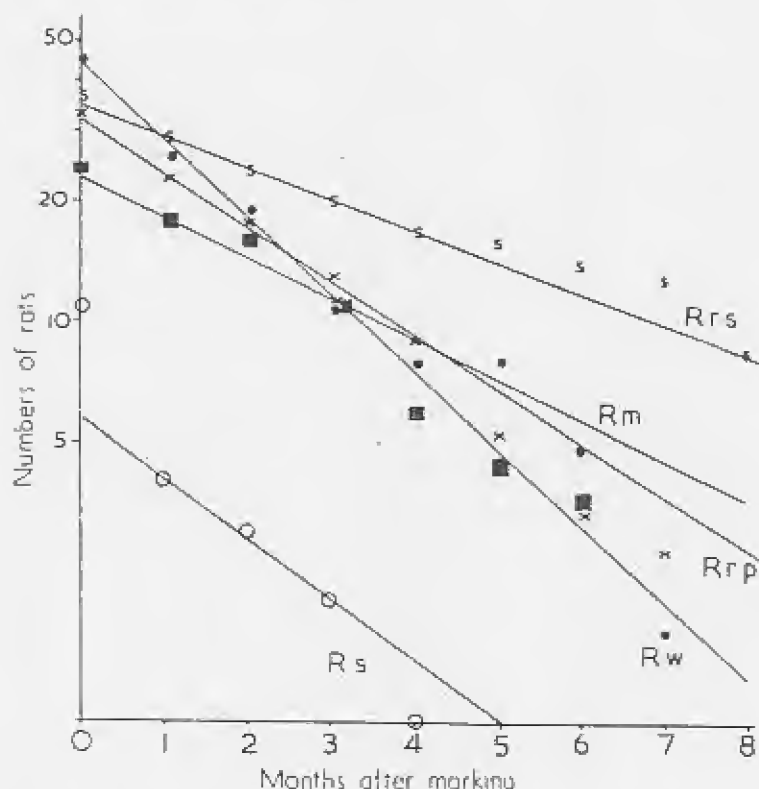

Fig. 7. Survival of marked Forest rats. Numbers of rats marked and recovered, on a logarithmic scale. At month 0 is plotted the number marked, at month 1 the total number recovered, at 2 the total number recovered after the first month, at 3 total recovered after the second month and so on.
Rrs (s), *R.r. surifer*; Rrp (x), *R. rajah pellax*; Rm (squares), *R. mülleri*; Rw (dots), *R. whiteheadi*; Rs (o), *R. sabanus*, all from Forest experiment.

Fig. 7 is of the forest rats, *R. sabanus, R. mülleri, R. whiteheadi,* and the two forms of *R. rajah* (*pellax* and *surifer*). Fig. 8 is of the grassland rats: *R. exulans* (crosses) from the "Pylon" area (ReP), and from the "Stream" and "House" areas combined (R.e.S. & H.); *R. whiteheadi* (dots) from all three areas; and *R.r. argenti-venter* (*a*'s) from all three. Fig. 9 is of various populations of *R.r. jalorensis,* from "Spooner Rd," from the "Pylon" and "Stream" areas combined, from "House", and from "Taylor Rd".
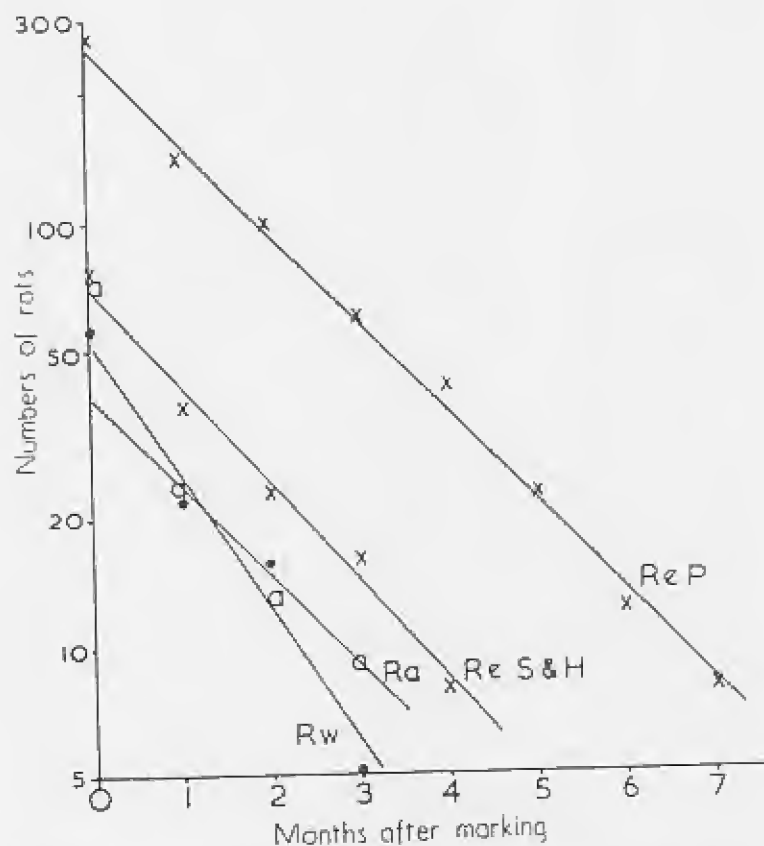

Fig. 8. Survival of marked scrub and grassland rats. As fig. 4, numbers on logarithmic scale, 0 . . . number marked, thereafter number recovered after successive months.
ReP (x), *R. exulans* from Pylon experiment, ReS&H (x), *R. exulans* from Stream and House experiments combined; Ra (a). *R.r. argentiventer* from all areas; Rw (dots), *R. whiteheadi* from all scrub areas.

Table 7 summarises the survival rates read from these diagrams, both as survival rate per month, and as mean expectation of life (that is, the average length of life of the population measured by finding the time by which the population sinks to $1/e$ of its former value).

TABLE 7

SURVIVAL ESTIMATE FROM MARKED RATS

Survival, as rate per month, and mean length of life in months, calculated from the records of marked rats shown in figs. 7–9 and the results of applying a correction of half the period of the trapping cycle.

| Species and Population		No. of rats marked	Survival rate per month	Mean length life (months)	Trapping cycle (months)	"Corrected" Mean length life	Survival rate
R.r. jalorensis							
Spooner Rd.	..	99	0·87	6·9	1·0	7·4	0·87
Taylor Rd.	..	14	0·78	4·0	0·8	4·4	0·80
House	..	29	0·76	3·6	2·4	4·8	0·81
Pylon & Stream	..	198	0·68	2·6	2·0	3·6	0·76
R.r. argentiventer	..	74	0·62	2·1	2·0	3·1	0·72
R. exulans							
Pylon	..	282	0·61	2·0	2·4	3·2	0·73
Stream & House	..	78	0·57	1·8	2·0	2·8	0·70
R. whiteheadi							
P.H.S.	..	58	0·49	1·4	2·0	2·4	0·66
Forest	..	45	0·63	2·2	2·4	3·4	0·75
R. mülleri	..	24	0·80	4·4	2·4	5·6	0·84
R. rajah surifer	..	36	0·83	5·3	2·4	6·5	0·86
R. rajah pellax	..	41	0·72	3·1	2·4	4·3	0·79
R. sabanus	..	11	0·71	2·9	2·4	4·1	0·78
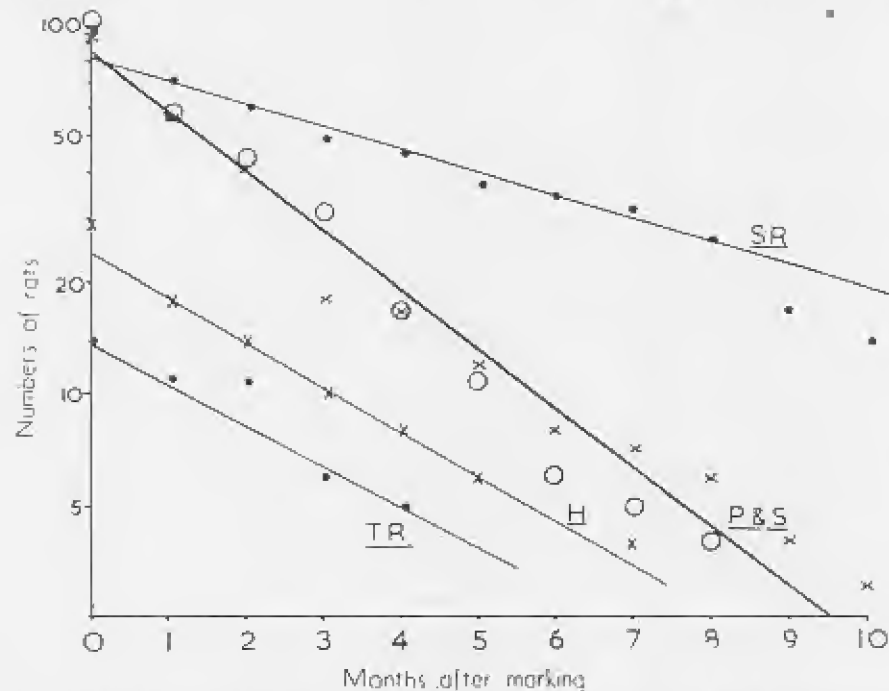
Fig. 9. Survival of marked *R.r. jalorensis*. As figs. 4 and 5, for populations of *R.r. jalorensis* from different experiments. *SR* (dots), from Spooner Road; *P&S* a single regression line for the points from *Pylon* (x) and *Stream* (O) experiments; *H* (x), from House experiment; *TR* (dots), from Taylor Road experiment.

Possible errors in estimation

1. **Emigration.** Evidence will be adduced in a later paper that the rats in fact spend most of their life within a fairly small area. Occasionally they appear to leave their home range and go elsewhere. Such events, however, appear to be uncommon, although there is some evidence that they do occur. Marking records also suggest that long range wanderings may occur in some species, thus a single specimen of *R.r. argenti-venter*, normally confined to grassland, has been trapped in forest a kilometre from the nearest grassland, and a specimen of *R.r. diardii*, normally confined to houses, has been trapped in scrub at least half a kilometre from the nearest house (a squatter's hut). Such emigrants would appear as non-survivors in marking experiments and would thus cause the survival rate to be under-estimated.

2. **Death of marked rats.** Although the marking of rats has no obvious effect upon them, it is possible that it does in fact increase the death rate. This could happen by increasing the susceptibility to infection as a result of the marking and of minor damage caused by the trap (to tail-tips and noses). Rats trapped several days in succession do lose weight so that slight starvation (the refusal of food in cages) is a possible factor. Furthermore, rats are released during the day, and this may cause slight increase in the chance of predation. The effect of this would be to increase the death rate of the marked animals so that the measured rate, although true for the marked population, would not be true for the population as a whole, and the survival rate would be under-estimated.

3. **Trapping cycle.** With the system used, the traps are laid according to a programme which ensures that a trap is laid at each point once in each cycle of trapping. The cycle is arranged so that traps are laid at adjacent points, well within the normal range of the rat, at intermediate times, but it is possible, with ranges marginal to the trapping area, that only one trap or one line of traps falls within the normal range. In that case the rat will be exposed to trapping only for one week in each cycle. If the rat dies within the interval its last appearance will be allotted to the beginning of the cycle instead of to some point within it and the survival rate would be under-estimated. We may apply a maximum correction by adding a period equal to half a trapping cycle to the mean length of life. This correction is applied in table 7 and the corresponding survival rates worked out. Where data are obtained from two areas with different cycles, a mean value of the cycle is used.

4. **Short experiments.** Rats occasionally reappear after a long absence (several months). If the experiment had been discontinued during the time, such rats would be recorded as non-survivors after the last appearance. This sort of error will be of importance only in short experiments, such as that at "Taylor Road" and at "Forest". For the other experiments a six month interval without record has been allowed before any rat has been recorded as a non-survivor. Unfortunately all the records for the five species of forest rat (Fig. 4) are derived from the "Forest" mark-recapture experiment, and all may be considered underestimated. This effect will be emphasised by a long trapping cycle and the correction applied above will help to compensate for it.

5. **Other errors.** Four possible sources of error have been considered, each of which would cause the survival rate to be under-estimated and which can, therefore, be

allowed for by a correction as suggested in paragraph 3. The fifth source is more diffi- cult to assess. It has been assumed in these calculations that p, the probability that a rat will be recaptured at any time after a particular date, remains constant. This may or may not be true. It is quite possible that p increases with time; either because a first trapping (at which the rat is marked) produces a temporary trap-shyness, thus reducing the chance of recovery soon after marking, or because repeated trapping produces a liking for traps, which would increase the chance of recovery with time. Either of these causes, by producing an increase of p with time, would cause the recovery curve to be concave upwards. Another possibility is that p may decrease with time as repeated trapping may induce a cumulative trap shyness. This should produce a curve which was concave downwards. In fact there is no sign of either departure from a straight line, and the possibility is ignored.

A comparison of survival and reproduction rates. We now have estimates of the survival rates of these rats obtained by two different methods which are reasonably in agreement. It remains to be seen if these rates are also in agreement with the pregnancy rates for the species given in the two earlier papers (Harrison 1951a, and 1955). If the population is stable, and that assumption is being made here, then the total number of rats dying in unit time will be equal to the total number born, that is the death rate and birth rate will be equal so long as these are both calculated on the whole population. It has been assumed that the death rate is uniform for all ages, and therefore the death rate calculated above will be the same as the rate for the whole population; the death rate being, of course, one minus the survival rate.

Estimation of the birth rate. A birth rate has not yet been calculated. In the earlier papers estimates were made, from the records of animals examined, of the pregnancy rates, mean embryo numbers, and sex ratio, and from these a "reproduction figure" was calculated, being the number of embryos per hundred rats (of both sexes) examined. To calculate a birth rate from this it will be necessary to estimate the period of visible pregnancy, the loss of embryos and the number of still births.

The period of visible pregnancy is not known for any of the rats considered. For *R. norvegicus* it appears to be of the order of 18 days (Perry 1945) and there is nothing to suggest that the gestation period of these rats differs widely from that species, so a period of 18 days (0·6 months) is taken as a first approximation.

The loss of embryos, again, must be largely guess work. Table 8 shows for each species, the mean litter size for the youngest and the oldest embryos respectively (i.e. of the numbers in the lowest and highest weight groups) and, in the last column, the mean for the oldest embryos is expressed as a mean of all litters. Clearly there is a reduction, although how much of this reduction is due to larger litters having embryos of smaller average size is difficult to assess. However the mean of all these ratios (87 per cent) can be taken as an estimate of the loss of embryos for all species.

The numbers of nests found with litters intact has been too small to provide any estimate of the usual number born alive, and some other estimate must be used. A study of a domestic colony of *R. norvegicus* by Dewar (1945) gives a rate of 83 per cent survival of the total number of nestlings born. Combining these two estimates of 87 per cent survival of embryos and 83 per cent survival of nestlings we get a ratio of 72 per cent between nestlings and embryos and this estimate is used below. Leslie *et al* (1952) in their study of *R. norvegicus* in the corn-ricks obtained an embryo number of 9·036 and a mean litter size of 7·0 in round figures, a ratio of 78 per cent.

J. L. HARRISON

TABLE 8
INTRA-UTERINE MORTALITY

Mean embryo numbers of litters containing the smallest (youngest) and largest (oldest) embryos, with the ratio between the latter and the mean of all litters.

Species	Mean embryo number (embryos/litter) youngest (lowest weight group)	oldest (highest weight group)	Ratio of oldest to mean of all litters per cent
Chiropodomys gliroides	2·3	2·0	87
R.r. diardii	6·7	5·2	91
R.r. jalorensis			
Oil Palm	4·0	3·2	91
Forest	5·2	5·4	100
R.r. argentiventer	6·0	6·0	100
R. exulans	5·0	4·2	93
R. mülleri	4·0	2·6	69
R. whiteheadi	3·3	2·9	97
R. rajah	5·6	2·8	85
R. sabanus	5·0	2·5	81
R. canus	4·3	2·0	67

Mean ratio .. 87

The reproduction figure is worked out on all rats examined. Young rats however, either are not trapped, or can escape from the trap, and so are not counted. The reproduction figure, therefore, is worked out on a population less than the whole population by the number of rats in these early age groups. If the survival rate is s and the age which the rat is first captured is a, then the reproduction figure is calculated on a population Ns^a instead of N. There will be no pregnancies among these very young rats, so the reproduction figure can be corrected by multiplying it by the value s^a. The value of a is estimated from tables 1 and 2 and the weights at which rats are first trapped.

The birth rate which we need, that is the ratio of live births to total population, can, therefore, be estimated from the reproduction figure by multiplying by the factors 30/18 for visible pregnancy, 72 per cent for deaths *in utero* and at birth, and s^a for the population on which it was calculated, that is a final factor of:—

$$\frac{30}{18} \times \frac{72}{100} \cdot s^a = 1 \cdot 2 \, s^a$$

This is done in table 9 and the result compared with the death rate. It will be seen that, on the whole, the agreement is reasonably close; remembering that the "birth rate" is derived from the reproduction figure largely by guesswork. For ease of reference, agreement to within 10 per cent is marked ($+$) and within 5 per cent is marked ($++$). The rates derived from the marking experiments (corrected) give a decidedly better agreement than those from the weight estimation, with the notable exception of those for *R.r. argentiventer*, in which the survival rate from the marking experiments is clearly much too low.

TABLE 9

A comparison of the death rates, estimated from the marking experiments (M) and from the weight distribution (W) with the "birth rate" estimated from the reproduction figure (r) and the age at first capture (a).

Species	Method	Habitat	Survival rate s %	Age at first capture a (months)	Reproduction figure r %	Birth rate $1·2rs^a$ %	Death rate $(1-s)$ %	Agreement
Chiropodomys gliroides	W	forest	96	2	14	15	4	
R.r. diardii ♀	W	town	83	2	47½	38	17	
♂			80	2			20	
R.r. jalorensis	W	oil palm	89	2	21·8	21	11	+
	W	scrub	85	2	36[*]	31	15	
	M	SR	87	2	21·8[†]	20	13	+
	M	P & S	76	2	36?	25	24	++
R.r. argentiventer	W	grass	93	2	13·7	14	7	+
	M	P S H	72	2	13·7	9	28	
R.r. jarak	W	Island	90	2	12·1	12	10	++
R. exulans	W	grass	85	3	51	38	15	
	M	P	73	3	51	24	27	++
R. mülleri	W	forest	93	2	27	28	77	
	M	F	84	2	27	23	16	+
R. bowersi	W	F	93	2	15	16	7	+
R. whiteheadi	W	forest	78	2	40	29	22	+
	M	F	75	2	40	27	25	++
	M	P H S	66	2	40	21	34	
R. rajah, all	W	forest	92	2	15	15	8	+
R. rajah surifer	M	F	86	2	17	15	14	++
R. rajah pellax	M	F	79	2	13	10	21	
R. sabanus	W	forest	93	1	22	24	7	
	M	F	78	1	22	21	22	++
R. canus	W	forest	90	2	24	23	10	

Conclusion. The object of the present investigation was to obtain information about the survival of rats. The information available suggests that the survival rate is approximately constant, whatever the age, and that the information can thus be adequately summarised by giving merely a mean survival rate. This is done in table 10, where the best estimates from table 9 are assembled and expressed as (a) survival rate per month, (b) mean length of life, and (c) "effective maximum" length of life, being the maximum of 95 per cent of the population (that is the age which only 5 per cent can be expected to survive).

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[*] The value of the reproduction figure for *R.r. jalorensis* from "scrub" is a new value, not published in the papers mentioned, and derived from all rats, whether collected in "forest", which is in fact the clearings of the aborigines, or wasteland.

[†] The reproduction rate for Spooner Road is taken as that of the oil palm rats, and that for Pylon and Stream as forest.

TABLE 10

SUMMARY OF SURVIVAL FIGURES

The figures given are those showing best agreement in table 9, or figures arbitrarily corrected to give agreement. The figures in the last column are the maximum periods for which marked rats have been recovered, the two highest records being given. For the forest rats the period is shown as 10+ to indicate that the rat was observed during 10 months and was still being recovered when the experiment was discontinued.

Species		Survival rate per month	Length of life in months		
			Mean	Effective maximum (95%)	Maximum recorded
Chiropodomys gliroides	..	0·88	7·8	23	—
R.r. diardii ♀ ♀	..	0·75	3·5	10½	—
♂ ♂	..	0·72	3·0	9	—
R.r. jalorensis					
sheltered	..	0·88	7·8	22	26, 19
scrub	..	0·76	3·6	11	14, 10
R.r. argentiventer	..	0·85	6·2	18	4, 3
R.r. jarak	..	0·90	9·0	28	—
R. exulans	..	0·73	3·2	10	9, 8
R. mülleri	..	0·84	5·6	18	10+
R. bowersi	..	0·85	6·2	18	—
R. whiteheadi	..	0·75	3·5	10	9+
R. rajah	..	0·86	6·5	20	10+
R. sabanus	..	0·78	4·1	12	—
R. canus	..	0·82	5·0	15	—

The estimates used are those which give best agreement with the estimated birth rate, but for *Chiropodomys gliroides*, *R.r. diardii*, *R. bowersi*, and *R. canus*, for which only the weight estimation was available, that estimate has been reduced by 8 per cent, the mean of all differences between weight estimates and those marking estimates which give a good fit. Such a reduction, in each case, gives a good agreement with the estimated birth rate. The same method has been applied to *R.r. argentiventer*, for which the estimate from marked rats is clearly too low.

In the last column is shown the two maximum periods for which a marked rat has in fact been known to live. Again with the exception of *R.r. argentiventer*, the agreement with the calculated "effective maximum" is close.

The figures must justify themselves by their consistency, and with the exception of *R.r. argentiventer* they are reasonably consistent. It will be seen from figures 7 to 9 that *R.r. argentiventer* and *R. sabanus* are the only two species for which the number marked (*N*) differs greatly from the number represented by the point at which the regression line cuts the zero axis. This indicates that p is small compared with s, and that the chance of recovery of a marked rat of these species is small compared with the chances for other species. For *R. sabanus* the reason for this is clear. As will be explained in a later paper, the area "Forest" in which the marking experiments were carried out was not favourable to this species, and most of the specimens marked evidently had ranges outside the experimental area. An undue proportion were therefore marked and never seen again. *R.r. argentiventer*, however, clearly ranged over the experimental area, and it seems that either the species is unusually "trap-shy", or else that it has an unusually large range, or is addicted to wandering, as suggested, on other grounds, in an earlier paper (Harrison 1951).

It should be noted that the species with the lowest survival rates, *R.r. diardii*, *R.r. jalorensis*, *R. exulans*, and *R. whiteheadi*, are the very species which can live in scrub, cultivation, and urban conditions. Clearly a low survival rate is not a disadvantage, rather it should be looked upon as the corollary of a high birth rate, indicating a species which can most quickly build up a large population and occupy new territory.

Summary

1. For the six years 1948–54 rats in the neighbourhood of Kuala Lumpur, Selangor, Federation of Malaya, have been studied by routine collection (primarily for parasites), by marking and recapture, and by keeping in captivity. The species for which sufficient data have accumulated are the Tree Mouse *Chiropodomys gliroides*, the forest rats *Rattus mülleri*, *R. bowersi*, *R. whiteheadi*, *R. rajah*, *R. sabanus*, and *R. canus*; and the commensal species *Rattus exulans*, and *Rattus rattus* in the forms *R.r. diardii*, *R.r. argentiventer*, *R.r. jalorensis*, and *R.r. jarak*.

2. The central part of Malaya has an unusually uniform climate, and the rats exhibit no breeding season. The size of a rat can, therefore, be related to its age, and tables of weight and age are given founded partly upon mark-recapture experiments, and partly upon caged animals.

3. The weights at different ages are applied to the weight distribution of a large random collection to obtain life tables which are expressed graphically. It appears that, at least for the first few months of life, the survival rate is constant.

4. The survival rates of rats marked at different ages are compared, and no significant differences are found.

5. Results of marking experiments are, therefore, consolidated, and treated graphically to give an estimate of mean survival rates.

6. The survival rates obtained by these two methods are compared with one another and with the reproduction rate estimated from data previously published. Estimates from the weight distribution are fairly consistently higher than those from marking, which latter give close agreement with the birth rates.

7. A summary of estimated survival rates is given for the twelve species.

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